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Source: The Wilson Journal of Ornithology, 128(1):97-107.

Published By: The Wilson Ornithological Society

DOI: <http://dx.doi.org/10.1676/wils-128-01-97-107.1>

URL: <http://www.bioone.org/doi/full/10.1676/wils-128-01-97-107.1>

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AMERICAN ROBINS (*TURDUS MIGRATORIUS*) AND CEDAR WAXWINGS (*BOMBYCILLA CEDRORUM*) VARY IN USE OF CULTIVATED CHERRY ORCHARDS

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ABSTRACT.—Some fruit-eating bird species commonly consume cultivated fruit. Species-specific variation in diet preferences could result in varying use of orchards and impacts on the fruit-producing industry. However, species-specific studies of avian orchard use are lacking, particularly throughout the fruit-growing season. Our objectives were to quantify the frequency of daily bird visits to orchards and the amount of time birds spent visiting orchards each day over the fruit-ripening season. Birds are well-documented consumers of cultivated sweet cherries (*Prunus avium*), which are relatively high in sugar and low in proteins and lipids. American Robins (*Turdus migratorius*) and Cedar Waxwings (*Bombycilla cedrorum*) are common fruit-consumers in sweet cherry orchards. Robins often consume larger proportions of invertebrates and prefer lipid-rich fruits, while waxwings choose sugary fruits. Given these species-specific diet differences, we hypothesized waxwings would spend a greater proportion of days and more time each day in cherry orchards, compared to robins. We used radio telemetry to track the habitat use of 25 American Robins and 17 Cedar Waxwings in sweet cherry orchards of Michigan. Over their respective radio-tracking periods, waxwings visited orchards a greater percentage of days than robins (waxwings: mean = 21%, SD = 22; robins: mean = 6%, SD = 4). In addition, waxwings visited orchards for more time each day. Differences in diet preferences and nutritional physiology may translate into species-specific patterns of habitat use for birds in fruit-rich environments. Received 4 February 2015. Accepted 2 August 2015.

Key words: American Robin, Cedar Waxwing, cherry, foraging, habitat use, orchard, telemetry.

Animals are expected to forage where and when they can obtain sufficient accessible and nutritious foods (Hengeveld et al. 2009). Orchards offer rich patches of foraging habitat with abundant food resources for birds, which may lead to conflicts with orchard growers (Simon 2008). Growers experience lost yields and often implement costly techniques to mitigate bird consumption of crops (USDA 1999, Anderson et al. 2013). Fruit growers in New York, Michigan, and the Pacific Northwest have reported yield losses up to 31% in cherries, 18% in blueberries, and 9% in wine grapes because of birds; these losses amount to tens of millions of dollars (Anderson et al. 2013). Knowledge of foraging patterns of avian frugivores in and around orchards can thus offer crop producers valuable

information for mitigating bird consumption of crops through targeting species and times when fruit loss is greatest (Dolbeer et al. 1994, Somers and Morris 2002, Tracey et al. 2007). For example, bird consumption of blueberries is greater in early ripening varieties; such information could allow growers to identify fruit varieties that ripen later in the season and reduce the potential for avian crop consumption (Tobin et al. 1991).

Birds are well-documented consumers of cultivated sweet cherries (*Prunus avium*) (Curtis et al. 1994, Lindell et al. 2012), but neither the frequency nor length of bird visits to commercial cherry orchards over the growing season have been established. A limited understanding of the orchard use and behavior of cherry-consuming species has hindered our ability to develop effective management programs that minimize costs of bird activity in orchards (Tracey et al. 2007). Cherry orchards are attractive for fruit-eating birds because cherries are brightly colored, densely available, and have easily accessible pulp (Sallabanks 1993). Cherries are relatively sugar-rich fruits; >50% of dry pulp mass comprises sugars (Witmer and Van Soest 1998, USDA 2013b). The lipid and protein contents among *Prunus* fruits (including cherries) are relatively low (<2%) compared to the protein content of other fruits (5%) or insects (Stiles 1993, Witmer and Van Soest 1998). Fruit consumption

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by birds is behaviorally and physiologically complex (Sallabanks 1993, Levey and Martínez del Rio 2001, Corlett 2011). Birds can discern nutritional differences among food types and make foraging decisions to meet energetic and nutritional needs (Lepczyk et al. 2000, Schaefer et al. 2003, Alan et al. 2013). Therefore, cherries may not appeal equally to all birds.

American Robins (*Turdus migratorius*; hereafter robins) and Cedar Waxwings (*Bombicilla cedrorum*; hereafter waxwings) are highly frugivorous (Wheelwright 1986, Witmer 1996). These species are also responsible for a relatively high proportion of observed avian cherry consumption compared to other species, (e.g., American Crow [*Corvus brachyrhynchos*], Common Grackle [*Quiscalus quiscula*], and European Starling [*Sturnus vulgaris*; Lindell et al. 2012]). Fruit comprises ~57% of the annual diet of robins, in addition to large proportions of invertebrates, while waxwings' diet contains ~84% fruit (Witmer 1996). Robins more efficiently assimilate and prefer fruits that are relatively high in proteins and lipids and low in sugars (Stiles 1993, Willson 1994, Witmer and Van Soest 1998, but see Lepczyk et al. 2000). Waxwings more efficiently assimilate and show a preference for high-sugar fruits (Witmer and Van Soest 1998, Witmer 1998). Waxwings maintain body mass on fruit alone for extended periods, (e.g., up to 27 days; Holthuijzen and Adkisson 1984), despite fruit's relatively low protein content. In contrast, Levey and Karasov (1989) attempted a 10-day fruit-only feeding trial on captive robins but shortened the trial to 4 days as birds had already lost 10–14% of initial body mass. Waxwings feed their nestlings insects for approximately 3 days (Putnam 1949), after which fruit comprises 87% of food deliveries (Lea 1942), while robins provision almost exclusively with animal matter (Hamilton 1935), but older nestling robins may also receive fruit (Eaton 1914). Our previous work has revealed relatively little use of cherry orchards by robins and waxwings for invertebrate consumption and nesting activities, therefore, we focused this study on fruit consumption.

These species-specific patterns likely influence the frequency and length of foraging visits in orchards during the cherry-growing season. For certain frugivorous birds, orchards may become increasingly attractive as fruits ripen because sugar content increases and bird energy needs may be met more efficiently (Serrano et al. 2005). After harvest, orchards may no longer be viable

foraging habitat for avian frugivores, given the near-complete removal of fruit from trees (<10% of cherries remaining; M. Whiting, pers. comm.).

We used radio-telemetry to evaluate the use of cultivated sweet cherry orchards in Michigan by robins and waxwings. We hypothesized that waxwings would exhibit more intense use of cherry orchards than robins based on their diets. We predicted that, compared to robins, waxwings would 1) visit focal orchards on more days throughout the cherry season, and 2) spend more time each day visiting orchards. Further, given that sugar content increases as cherries ripen, we expected that 1) robins and waxwings would increase their use of orchards as harvest approached, and 2) that orchard use by both species would decline abruptly after cherries were harvested and fruit availability declined. For both of these expectations, we predicted a stronger effect for the more fruit-specialized waxwings.

METHODS

Study Area and Species.—We conducted the study in four sweet cherry orchards in Leelanau County, near Traverse City (44° 46' N, 85° 37' W), in northwest Michigan from June–September 2013 (Fig. 1). Leelanau County is a peninsula (land area = 900 km², water area = 5659 km²) extending into Lake Michigan and an agricultural region comprising many orchards (e.g., sweet and tart cherries, wine grapes, apples). As of 2012, orchards comprised 6% of the county land area, with sweet cherry orchards accounting for 2% of the county land area (USDA 2012). Other major crops and land cover types include alfalfa, mixed forests, and residential or developed areas (Lindell et al. 2012). The average rainfall during the 2013 fruit-growing season (Apr–Oct) was 54.9 cm (Northwest Michigan Horticultural Research Station 2013).

The mean distance between study sites was 5.1 km (range = 1.4–10.4 km). One site was located at the Northwest Michigan Horticultural Research Station (STA) and Cherry Bay (CB) Orchards, Inc. managed three sites (Table 1). In the study region, sweet cherry trees typically reach full bloom in early May; small green fruits are evident 20 days later, and cherries begin ripening 50–60 days after full bloom. Growers apply a variety of insecticides depending upon the target pest species, fruit growth stage, and product availability (W. Klein, pers. comm.). Products vary in required application frequency (e.g., from 3 days up to

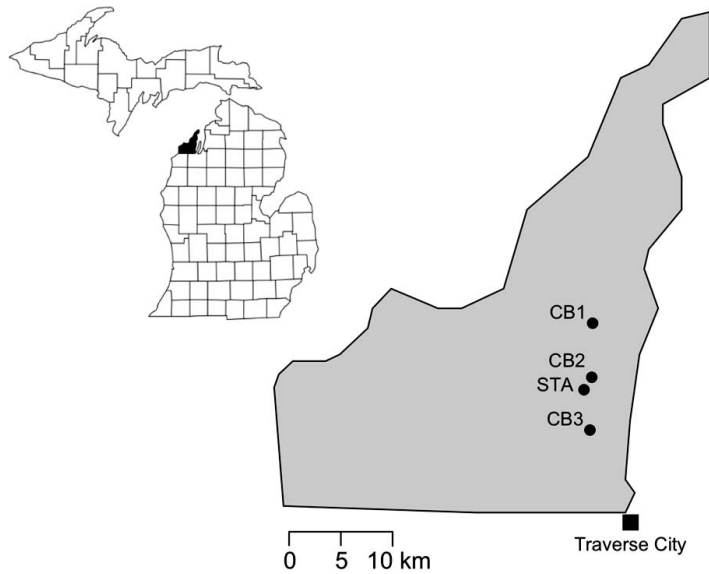


FIG. 1. Map of Michigan with Leelanau County identified (left). Map of Leelanau County with Traverse City and the four sweet cherry study orchards identified (right).

2 weeks) and the Michigan State University Extension provides recommendations for insecticide use to commercial fruit producers in the region. Orchard managers prune trees and mow grass occasionally throughout the growing period.

In Michigan, robins are abundant during the breeding season and typically arrive in March; most robins do not overwinter (McPeck 2011a). Robins begin nesting in April and May and commonly rear two broods (Howell 1942, McPeck 2011a). Waxwings are common in the study region where they travel and forage in small flocks year-round (McPeck 2011b). Waxwings generally arrive in Michigan by late May (although some overwinter). They are among the latest nesting birds in North America and nest in colonies in trees of various species including maple (*Acer* spp.), oak (*Quercus* spp.), and pine (*Pinus* spp.; Lea 1942,

Putnam 1949, Rothstein 1971). The majority of nesting occurs between mid-June and August (McPeck 2011b). Orchard growers in the study region do not remove nests from cherry trees during the growing season (growers may remove old nests during the winter; W. Klein, pers. comm.).

Capture and Radio Deployment.—We captured birds via mist nets in each study orchard and radio-tagged adult robins and waxwings between 1 June and 15 July. We typically opened nets by 0700 and closed them by 1600 EDT. We aged and weighed birds and determined sex using external breeding characteristics (i.e., presence of brood patch or cloacal protuberance; Pyle 1997). Waxwings did not exhibit external breeding characteristics, and sex could not be reliably determined. We fitted a metal band, plastic colored bands, and an A1055 radio transmitter from Advanced Telemetry

TABLE 1. Study area, 2013 harvest date, and land cover types immediately adjacent to (within 25 m of edge) orchard sites. The number and sexes (M: male, F: female, U: unknown) of American Robins (AMRO) and Cedar Waxwings (CEDW) caught at each sweet cherry orchard. Adjacent land covers were assessed visually at each site as part of a related study in 2013.

Orchard	Site area (ha)	Harvest	Adjacent land cover types	AMRO	CEDW
STA	3.84	19 July	Tart cherry, mowed grass, non-fruit crops, herbaceous (<1 m tall)	5 M, 3 F	8 U
CB1	2.6	11 July	Tart cherry, mowed grass, herbaceous (<1 m tall)	4 M, 3 F	3 U
CB2	11.6	10 July	Mowed grass, paved road, sweet cherry, non-fruit crops	2 M	
CB3	0.4	9 July	Tart cherry, paved road, herbaceous (<1 m tall)	5 M, 3 F	5 U

Systems Inc. (Isanti, MN, USA) on 25 robins and 17 waxwings that appeared in good condition and were of sufficient size to wear the 0.9-g radio transmitter and harness ($<3\%$ of bird body mass). We used 1-mm elastic cord and the figure-eight leg-harness method to attach transmitters (Rappole and Tipton 1991). Transmitters broadcasted at a pulse rate of 30–34 pulses per min within a frequency range of 164.00–165.66 MHz; expected battery life was 50–60 days. After radio deployment, we gave birds a 2-day acclimation period to permit a return to normal behavior prior to data collection. Radio-tags from two waxwings were recovered during the study; we suspected both birds were depredated. We had orchard use data from both individuals and included these data in analyses.

Data Collection.—To track orchard use, we placed one stationary data receiving system in each study orchard, away from objects that could dampen or block incoming signals. We installed receiving systems during 15–20 June 2013 and retrieved them on 11 September 2013. To assemble stationary systems, we encased a programmable, R4550 data-logging signal receiver from Advanced Telemetry Systems Inc. (Isanti, Minnesota, USA) powered by a deep-cycle battery in a large plastic container and cabled the receiver to a six-element Yagi antenna bolted to an elevated mount of 3 m height (Homan et al. 2013). Prior to data collection, we synchronized time and date for all receivers.

The receivers scanned through a list of all radio frequencies associated with birds, remaining on each frequency for 6 secs, for 24 hrs per day throughout the study. If a frequency was detected during these 6 secs, the receiver monitored that frequency for 50 secs and recorded the date, time, and strength of the strongest signal (a function of distance between the receiving antennae and a bird's transmitting antenna) detected for that bird during the 50 secs. If a particular frequency was not detected, the receiver scanned for the next frequency. To promote independence among data for a given bird, receiving systems stored only the data record with the strongest signal detected over every 10-min period throughout the day. This record also included the number of radio pulses recorded for that bird during the 10-min period. The number of radio pulses reflected the number of times (i.e., for how long) a bird's transmitter emitted the signal during the 10-min period. The strength of a bird's signal did not affect the receiver's ability to detect other birds in the area.

To ensure that radio-tagged birds were still in the region during the study, we searched the area 5–7 days per week using a vehicle roof-mounted, rotatable set of dual 6-element Yagi antennae. The tracking periods of individual birds could include days on which birds were not detected using orchards, but were located in the study region during mobile searches.

Data Preparation.—Telemetry data receiving systems can detect false signals from objects (e.g., solar flares, power lines, garage door openers) with frequencies similar to those in our study. We used Visual Basic for Applications with Excel to cull false records and extract valid data for analysis. Valid data were those with associated pulse rates of 28–34 pulses per min; this range accounted for fully functioning radio transmitters, as well as slower pulsing radios whose batteries had weakened. We determined a bird was using an orchard if the receiver recorded a signal strength ≥ 140 (maximum radio signal strength was 155). We conducted calibrations at each study site prior to deployment and determined that a signal of ≥ 140 would only register if a bird was in a study orchard. To calibrate orchard use, we affixed a radio transmitter to a 2-m long pole, stood with the transmitter extended into a tree to simulate a bird at 4–6 locations in each orchard, and recorded the signal strength detected by the receiving system at each location. The line of sight receiving distance of the stationary systems was ≤ 0.05 km (Homan et al. 2103).

Day-to-day and Within-day Orchard Use.—We evaluated bird use of cherry orchards in two ways. First, we quantified day-to-day orchard use by calculating the proportion of days a bird was within a focal orchard out of the total number of days in the bird's tracking period (defined as the first day after the bird's acclimation period through the last day a bird was detected in the study region; equation 1). We defined a day as only the daylight period (1 hr before sunrise through 1 hr after sunset). We calculated one day-to-day orchard use value for each bird. Second, we quantified within-day orchard use to determine the amount of time birds visited focal orchards on a given day (equation 2). To quantify within-day orchard use, we first identified the length of the daylight period for each day of the study and divided this period into 10-min time blocks. We then quantified the number of 10-min time blocks in which a bird was in an orchard on a given day and divided this by the total number of 10-min blocks of that day

TABLE 2. Generalized liner mixed models exploring the relationships between within-day orchard use of American Robins and Cedar Waxwings, relative to species, orchard, and days-to-harvest, as well as parameter numbers (k), deviance (Dev), AICc, Δ AICc, and model weight (w_i) values. All models also included individual bird as a random effect. The star symbol denotes a two-way interaction term between covariates.

Model	k	Dev	AICc	Δ AICc	w_i
Species	3	382.7	389.9	0.0	0.64
Days-to-harvest + Species	4	382.3	392.6	2.6	0.17
Orchard + Species	5	380.9	394.4	4.5	0.07
Days-to-harvest	3	387.3	394.6	4.7	0.03
Orchard	4	385.9	396.1	6.2	0.03
Days-to-harvest + Orchard + Species	6	380.8	398.1	8.2	0.01
Days-to-harvest + Orchard	5	385.5	399.1	9.1	0.01
Days-to-harvest + Orchard + Species + Species*Orchard	8	374.3	400.5	10.6	0.00
Days-to-harvest + Orchard + Species + Species*Days-to-harvest	7	380.1	401.5	11.6	0.00
Days-to-harvest + Orchard + Species + Species*Orchard + Species*Days-to-harvest	9	374.0	405.9	15.9	0.00

(equation 2). An individual could have multiple within-day orchard use values. We report values for day-to-day and within-day orchard use as percentages.

Day-to-day orchard use =

$$\frac{\text{number of days bird detected in orchard}}{\text{number of bird's total tracking days}} \quad (1)$$

Within-day orchard use =

$$\frac{\text{number of 10-min time blocks in orchard on one date}}{\text{number of time blocks in date's daylight period}} \quad (2)$$

Statistical Analyses.—The proportion values for day-to-day orchard use were right-skewed, so we applied a logarithmic transformation. We approximated the log-transformed day-to-day orchard use data using a normal distribution with equal variances, which satisfied assumptions for a two-sample Student's t -test. We determined if day-to-day orchard use data from male and female robins could be pooled. To account for sample size differences in males (9) and females (3), we used bootstrapping techniques to select three samples from males at random, with replacement, to compare with females. We ran 1000 iterations of the sampling and t -test procedures and applied the false discovery rate approach to correct α for multiple statistical comparisons (Benjamini and Hochberg 1995). We used a two-sample Student's t -test to evaluate differences in the day-to-day orchard use of robins and waxwings.

We constructed generalized linear mixed models (GLMM) with a binomial distribution, a logit

link function, and bird as a random effect to analyze within-day orchard use. We first used a GLMM with sex as a fixed effect and individual bird as a random effect (to account for some birds having multiple within-day orchard use values) to determine whether male and female within-day orchard use data could be pooled. A binomial distribution was appropriate for the within-day use data because we calculated these values as the proportion of 10-min time blocks in a given day in which a bird was in an orchard. The total number of time blocks in a day served as the number of trials for these models. We constructed 10 GLMMs to assess the effects of species and days-to-harvest on within-day orchard use (Table 2). We calculated the variable days-to-harvest for each date by subtracting this date from the harvest date of the relevant orchard. We included the orchard in which a bird was detected by a receiving system as a covariate for which we had no *a priori* expectation but which might have confounded the influence of days-to harvest. We used the Akaike Information Criterion corrected for small sample sizes (AICc) for model selection; we identified the best-fit model as that with Δ AIC value <2 (Burnham and Anderson 2002). We performed analyses in R statistical software (R Core Team 2014), using 'lme4' (Bates et al. 2015) and 'AICcmodavg' (Mazerolle 2015) packages.

RESULTS

Study Demographics.—We outfitted 25 robins (16 males, 9 females) and 17 waxwings (sexes unknown) with radio transmitters (Table 1). Among all radio-tagged birds, we did not detect

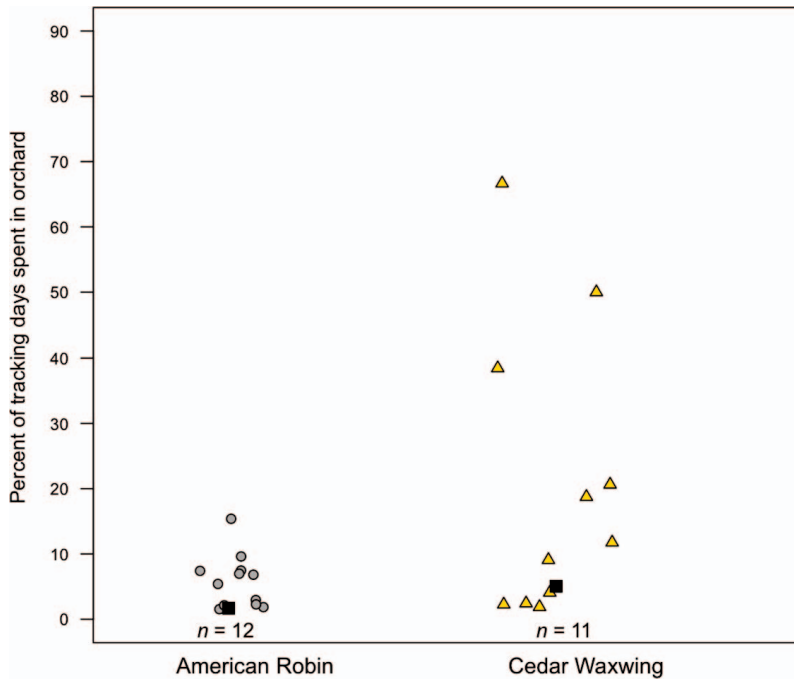


FIG. 2. Percent of days American Robins and Cedar Waxwings visited cherry orchards relative to their respective tracking periods. Waxwings visited orchards for a greater proportion of their total tracking days than robins. Data represent day-to-day use values ($n = 23$). Black squares represent sample means. Data are untransformed and are offset for visual clarity.

19 individuals (six male and seven female robins and six waxwings) in any of our study orchards after initial capture. Our sample population for analyses was comprised of 12 robins and 11 waxwings that used orchards STA, CB1, and CB3—no birds used CB2. Student's t -tests with bootstrapping showed no difference between male and female robins for day-to-day orchard use ($t = -0.50$, $P = 0.94$). The GLMM with sex as the fixed effect and individual bird as a random effect suggested that within-day orchard use did not differ between male and female robins ($z = 0.32$, $P = 0.75$). Therefore, we pooled data for the two sexes.

Day-to-day and Within-day Orchard Use.—Among robins and waxwings who used cherry orchards ($n = 23$), we detected individuals somewhere in the study region for a mean of 40.8 days ($SD = 19.5$), while birds visited focal orchards for a mean of 3.3 days ($SD = 3.0$), or 13% ($SD = 17$). Waxwings visited orchards on a marginally greater percent of days throughout the season (mean = 21%, $SD = 22$) than robins (mean = 6%, $SD = 4$; $t = -1.97$ on log-transformed data, $df = 21$, $P = 0.063$; Fig. 2).

The best-fit model of within-day orchard use, according to AICc selection criteria, included species as the fixed effect and individual bird as a random effect ($r^2 = 0.46$; Table 2). Waxwings visited orchards a mean of 5% ($SD = 6$) of the daylight periods in orchards, while robins visited a mean of 2% ($SD = 2$). Waxwings spent significantly more time visiting orchards per day than robins (species = 0.88, $SE = 0.31$, $P = 0.005$; Fig. 3). Individual variation among birds explained 34% ($SD = 0.58$) of the variance in within-day orchard use.

The days-to-harvest and orchard covariates did not appear in the best-fit model of within-day orchard use (Table 2). The days-to-harvest covariate was retained in the second best model of within-day orchard use ($\Delta AIC = 2.6$). This model suggested a decreasing trend in within-day orchard use as harvest approached; however, this was not significant (days-to-harvest = -0.004 , $z = -0.57$, $P = 0.57$). Orchard use at the STA orchard declined slightly up to 20 days before harvest; orchard use then remained constant until after harvest (Fig. 4). Orchard use at CB1 and CB3 was seemingly constant across the entire study period (Fig. 4).

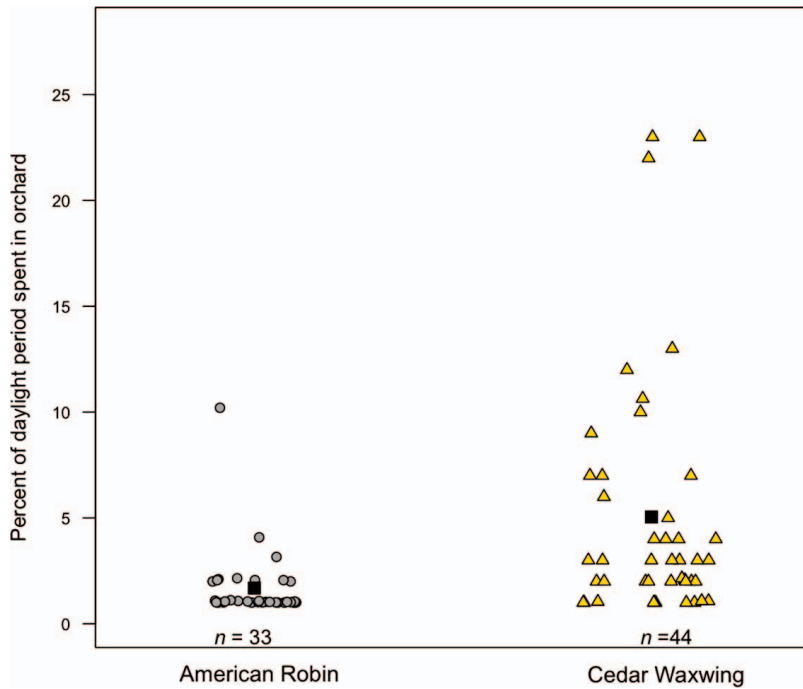


FIG. 3. Percent of the daylight period that American Robins and Cedar Waxwings visited cherry orchards on a given day. Waxwings visited orchards for more time each day than robins. Data represent within-day use values ($n = 77$) from a study population of 23 individual birds. Black squares represent sample means. Data are offset for visual clarity.

DISCUSSION

Robins and waxwings differ in fruit preference, nutritional requirements, and physiology (Levey and Karasov 1989, Witmer and Van Soest 1998). These differences translated into species-specific patterns of orchard use.

Day-to-day Orchard Use.—Our metric of day-to-day orchard use showed an insignificant but suggestive trend ($P = 0.063$) indicating that waxwings visited orchards a higher percentage of days throughout their tracking periods than robins. Fruit comprises a larger proportion of waxwing annual diets (Witmer 1996), and thus, waxwings take greater advantage of the abundant supply of cherries over the growing season, compared to robins. Robins, although predominantly frugivorous, typically consume and provision large proportions of animal matter to nestlings during the summer, while fruit consumption is higher in fall and winter (Wheelwright 1986). Therefore, a sweet cherry orchard may not be as valuable of a foraging habitat for robins, seeking protein-rich foods like insects and annelids, compared to waxwings. While it is possible that robins forage for non-cherry foods while visiting cherry orchards,

165 hrs of foraging observations yielded only six instances of robins consuming invertebrates but dozens of instances of cherry consumption (RAE, pers. obs.). Additionally, growers in focal orchards used insecticides regularly to diminish insect populations, potentially further limiting the value of cherry orchards for foraging robins. More study is needed to determine the relative proportions of fruit and invertebrates in the diet of robins in fruit orchards. Individual variation may also be a contributor to the patterns of day-to-day orchard use, as three individual waxwings appear to drive the relatively high day-to-day orchard use of waxwings, compared to robins.

Our hypothesized difference in day-to-day orchard use between robins and waxwings was insignificant, but suggestive, which could arise if robins used orchards more than expected while waxwings used them less. Robins may have used orchards more than predicted if orchards were near nesting sites, e.g., in windbreaks around orchards (Yahner 1982). In comparison, waxwing use of orchards may not have been particularly high if late-nesting waxwings were not yet tied to a breeding territory (Putnam 1949), and freer to

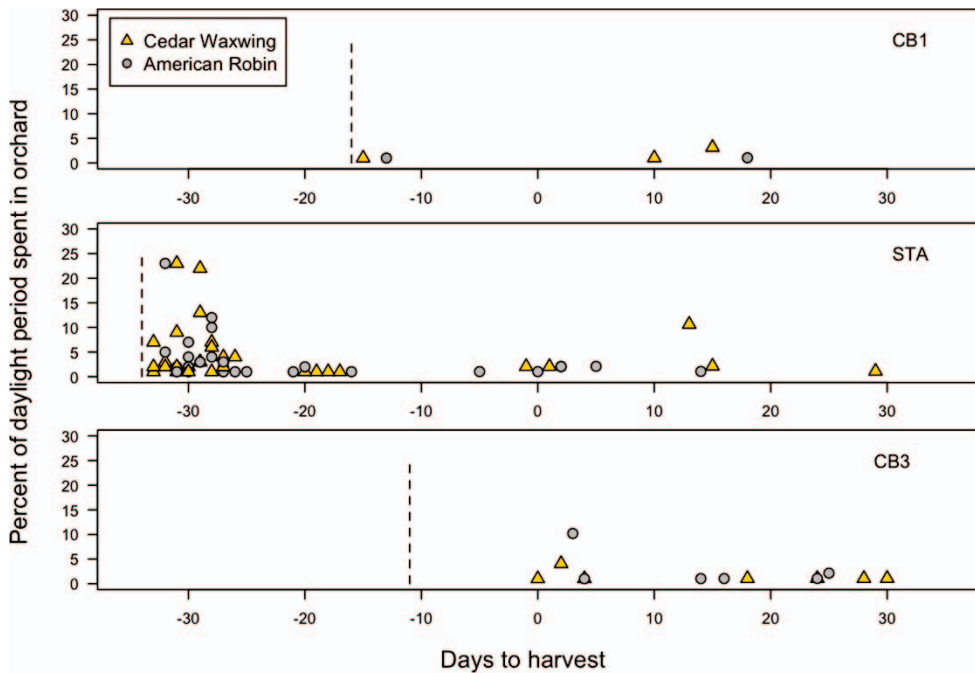


FIG. 4. Percent of the daylight period that American Robins and Cedar Waxwings visited cherry orchards on a given day relative to days-before-harvest. Data are separated by orchard (STA, CB1 and CB3). Data represent within-day use values ($n = 77$) from a study population of 23 birds. Dashed lines represent the first possible date of valid data collection for birds radio-tagged at each orchard. On the x-axis, zero represents the date of harvest for a given site.

travel among foraging patches than breeding robins. We conducted a preliminary, systematic search for nests in the study region that revealed very few, thus it is unlikely that robins and waxwings used cherry orchards for nesting.

Within-day Orchard Use.—Waxwings spent substantially more time visiting focal orchards than robins on a given day. Outside of the cultivated-fruit growing season, robins and waxwings also show differential timing of within-day fruit-foraging behavior (Chavez-Ramirez and Slack 1994). Wintering robins and waxwings in Texas spent 5 hrs and 8 hrs per day, respectively, feeding on Juniper berries (*Juniperus ashei*; Chavez-Ramirez and Slack 1994). Once nesting is underway, waxwings may spend more time visiting orchards than robins on a given day to gather fruit for nestlings. Waxwings provision chicks primarily with fruit and begin doing so as early as day 3 after hatching (Putnam 1949), where robins do not provision with fruit until chicks are older (Howell 1942 and references therein). Future studies could address the potential influence of nesting phenology on frugivore orchard use by

tracking breeding status, nesting, and brood rearing throughout the fruit-growing season.

We did not detect an influence of days-to-harvest on the amount of time birds spent visiting orchards. As cherries ripened, we expected birds to spend more time visiting orchards each day. In contrast to expectations, a temporal decline in within-day orchard use as harvest approached was evident for the STA orchard only. STA is a research orchard with dozens of sweet cherry varieties, including some early-ripening. Unlike other orchards in the region, multiple trees at STA had red and ripening fruit when our study began. Therefore, STA may have attracted birds early in the fruiting season (Nelms et al. 1990, Tobin et al. 1991). Cultivated orchards may provide fruit-eating birds with the majority of—or only—fruit options during this time. Waxwings consumed substantially greater proportions of early-ripening varieties of cultivated blueberries compared to later-ripening blueberries (Nelms et al. 1990).

Contrary to our expectations, birds used orchards after harvest. After harvest, some fruits remain on the trees ($< 10\%$ of the pre-harvest amount;

M. Whiting, pers. comm.) and ground. If focal orchards were near nesting sites and within the regular foraging ranges of radio-tagged birds, post-harvest orchard use may reflect birds' tendencies to forage close to nests (Swihart and Johnson 1986). Remaining fruits are still numerous, accessible, and visually appealing, and could attract frugivorous birds (Sallabanks 1993, USDA 2013a); robins were observed consuming cherries in trees and on the ground in post-harvest orchards in the study region (RAE, pers. obs.). As late-season nesting waxwings are likely provisioning offspring around or after cherry harvest, the remaining fruit in post-harvest orchards may serve as an important resource. Birds may also continue to use orchards after cherry harvest to forage for food unrelated to harvest (e.g., invertebrates); however, most cherry growers apply a post-harvest insecticide spray which may limit insect availability (W. Klein, pers. comm.).

Nearly half of our radio-tagged birds were detected in the area throughout the study but never used study orchards after the initial capture and acclimation period. Birds may have been captured as they traveled through an otherwise unused orchard. The home range sizes of robins are not well documented (Vanderhoff et al. 2014), although breeding robins have been known to forage up to 300 m from their nests (Knupp et al. 1977). Given the distance among our focal orchards (≥ 1.4 km) and their typical area (mean = 4.6 ha; SD = 4.9), robins captured at one orchard would not likely be detected using another, and robin foraging ranges in our study region do not contain more than a couple of cherry orchards. To our knowledge, the home range sizes of waxwings are unknown. We did not find any radio-tagged birds using multiple focal orchards. Captured birds may have avoided orchards if the capture experience itself served as a deterrent. We captured two male robins at CB2, but neither returned to that orchard; however, we later detected both individuals using the nearby STA orchard.

While we documented the frequency and length of visits to focal orchards, the extent to which robins and waxwings used other cherry orchards in our study region is unknown. Given that cherry orchards are widespread in the study region, it is very probable that robins and waxwings used non-focal orchards during the study period. If home ranges of robins and waxwings are large relative to orchard size, our study provides a conservative picture of avian use of cherry orchards in an orchard-rich landscape. If home ranges are relatively

small, it is possible that birds used non-focal orchards very rarely. Our results suggest that orchards might not be a predominant foraging habitat for frugivorous birds in this region. These uncertainties invite further study, particularly to track and evaluate avian habitat use in orchard landscapes with a more detailed resolution to determine frequency of use of non-orchard habitat and home ranges.

Bird use and consumption of agricultural crops is often viewed as problematic (Weatherhead et al. 1982, Anderson et al. 2013). However, use of these habitats by birds may provide ecosystem services to growers (Whelan et al. 2008) before and after harvest. Before harvest, avian consumption of crop-damaging invertebrates can increase the yield of cultivated crops (Mols and Visser 2002). For example, Great Tits (*Parus major*) reduced caterpillar consumption on cultivated apples and increased fruit yield (Mols and Visser 2002). After harvest, fruit often remains on the ground and can serve as vectors for infections such as American brown rot (*Monilinia fructicola*). This fungus can over-winter in fruits that have fallen to the ground and inoculate infections the following spring (Bush et al. 2015). Avian post-harvest consumption of cherries on the ground could reduce remaining fruits and limit the spread of infection. This and other potential benefits of avian fruit consumption deserve further study.

This work demonstrates that two prominent avian fruit-eating species differ in how intensely they use orchards over the fruit-growing season, likely as a result of the differences in their food preferences and reliance on fruit. Waxwings visit orchards on a greater proportion of days and spend more time within orchards each day than robins, and consume a relatively higher proportion of fruit compared to robins and other fruit-eating species (e.g., Common Grackles [*Quiscalus quiscula*] and European Starlings [*Sturnus vulgaris*; Lindell et al. 2012]). Waxwings are more likely to forage in groups than robins (Lindell et al. 2012) and have faster sugary-fruit assimilation rates than thrushes (Witmer and Van Soest 1998). Robins typically eat relatively little fruit during the breeding season compared to other times of year but show higher fruit consumption when foraging around orchards than in less-fruited habitats like meadows (Wheelwright 1986). Therefore, cherry orchards may serve as more important foraging habitat for more-frugivorous birds like waxwings than birds like robins who require protein-rich resources.

More work is needed to evaluate the extent to which birds foraging in orchards consume fruit versus other food sources like invertebrates.

ACKNOWLEDGMENTS

We thank K. Howard and M. E. Shave for field assistance. RAE would like to thank B. Bachelot for field assistance and many helpful comments on this manuscript. F. Otto of Cherry Bay Orchards allowed us access to orchards. We thank the staff of the Northwest Michigan Horticultural Research Station for use of orchards, equipment, and administrative support. The Specialty Crop Research Initiative of the USDA, Wilson Ornithological Society, and George J. and Martha C. Wallace Endowed Scholarship provided funding for this work. This study was approved by Michigan State University's Institutional Animal Care and Use Committee; approval number 05/11-107-00.

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